Zoogeography of West Indian Land Mammals

By George Gaylord Simpson

INTRODUCTION

The West Indies today are extremely poor in living native land mammals, so poor that discussion of their zoogeography on that basis alone would lack substance. There is, however, a considerable number of recently extinct land mammals known from caves and other deposits. Some of the deposits show a sequence from probable late Pleistocene onward, but the great majority if not all of the genera so preserved survived into the beginning of the geological epoch Recent. At the level of genera, at least, all may thus reasonably be taken as forming a single early recent fauna. Their zoogeography is discussed on that basis. This essay is not, in any case, concerned with species. The species are with a single exception (*Isolobodon portoricensis* on Hispaniola and Puerto Rico) endemic on each of the larger islands. Their geography has its own interest, but the zoogeography of the islands as a whole concerns the genera and higher categories. Discussion is, further, almost confined to the four main islands of the Greater Antilles: Jamaica, Cuba, Hispaniola, and Puerto Rico. The limited scope of this study excludes bats. Their zoogeography in the West Indies is of exceptional interest and is being studied by Koopman and others, but it is a separate topic. Animals known to have been introduced by man are of course also excluded.

The faunas in question are for the most part extinct, although recently so. They are certainly inadequately known, as is evident from the late recognition, essentially from a single specimen, of an order previously thought to be absent (Primates, see Williams and Koopman, 1952). Anything said now may be upset by new discoveries at any time. Much evi-

dence is negative, and negative evidence is here even more tricky than usual. West Indian zoogeography at present is more a matter of weighing sometimes nebulous probabilities than of drawing clear conclusions, and much must be frankly speculative. Still it is worth while to summarize what is known and to try to draw tentative conclusions.

Drs. Karl Koopman and Max Hecht, outstanding students of West Indian zoogeography, have kindly read this paper in manuscript and corrected several errors and oversights. They are not responsible for any remaining errors or for the conclusions drawn.

THE FAUNA

Table 1 lists the known orders, families, and genera and gives the distribution of the genera on the four main islands. The fauna is described or listed in many publications, of which the following are especially useful and, with their citations, lead to the whole literature: Allen (1911), Anthony (1925-1926), Hoffstetter (1955), Miller (1916, 1922, 1930), Miller and Kellogg (1955), Williams and Koopman (1951, 1952).

The outstanding peculiarities of this fauna are:

1. Small size in relationship to the area and diversity of the region.
2. Limited systematic scope, with only four orders and nine families.
3. Ecological unbalance, with no carnivores, ungulates, etc., and only a small range of adaptive types among the few groups that are present.
4. Extreme endemism on each island and in the island group as a whole.
5. A general faunal type or composition such as does not exist and quite surely never has existed on any mainland.

These peculiarities raise many questions, the first of which is the origin in time and space of the fauna or, rather, of its various elements.

ORIGIN OF THE WEST INDIAN NATIVE LAND MAMMALS

It is clear that land mammals reached the Greater Antilles at various different times and from various different places. The insectivores must be very ancient. They belong to endemic families and have no known relatives, living or fossil, within the Insectivora.[1] No insectivores are known from South America except for the recent invader *Cryptotis*, which has nothing to do with the case, and perhaps the Miocene *Necrolestes*, which may not be an insectivore and also has nothing to do with the Antillean groups. Insectivores were abundant in North America from late Creta-

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[1] Former reference to the Solenodontidae of various Oligocene North American genera (e.g., Simpson, 1945) seems on further study to be unjustified. It has also become evident that older suggestions of relationship with the Tenrecidae of Africa and Madagascar are probably incorrect.

TABLE 1

Genera of Land Mammals in the Greater Antilles

	Jamaica	Cuba	Hispaniola	Puerto Rico
Insectivora				
Solenodontidae				
Solenodon		×[a]	×	
Nesophontidae				
Nesophontes		+[b]	+	+
Primates				
Cebidae				
Xenothrix	+			
Edentata				
Megalonychidae				
Acratocnus		+	+	+
Megalocnus		+	+	
Mesocnus		+		
Microcnus		+		
Rodentia				
Cricetidae				
Oryzomys	+			
Heptaxodontidae				
Heptaxodon				+
Elasmodontomys				+
Clidomys	+			
Spirodontomys	+			
Speoxenus	+			
Quemisia			+	
?Octodontidae				
Alterodon	+			
Capromyidae				
Capromys		×		
Geocapromys	×	+		
Hexolobodon			+	
Plagiodonta			×	
?Capromyidae				
Isolobodon			+	+
Aphatraeus			+	
Echimyidae				
Brotomys			+	
Boromys		+		
Heteropsomys				+
Homopsomys				+
Proechimys				+

[a] Living.
[b] Extinct.

ceous onward and were especially varied in the early Tertiary. That is the most likely place and time for the ancestors of the two Antillean groups, although those ancestors have not been identified.

The megalonychids and heptaxodontids must also be old West Indian elements, but they are probably not so old as the insectivores. Both families have developed strongly differentiated endemic Antillean genera. The megalonychids could not be derived from any late Pliocene or Pleistocene mainland forms, aside from the fact that the span of the Pleistocene would probably be too short for such radical generic divergence. They could be derived from some South American Miocene or at latest early Pliocene sloths. Miocene dispersal to the Antilles from South America is most likely; although slightly later time and immediate origin from Central America are not wholly ruled out.

Among the rodents, the whole subfamily Heptaxodontinae is judged endemic to the Greater Antilles, but some Pliocene forms from Argentina have been doubtfully referred to it. In any case the ancestral group certainly lived in South America, where related rodents appear in the Miocene and are abundant in the Pliocene. Late Miocene or Pliocene dispersal from South America is a likely hypothesis. Again immediate Central American origin is not wholly excluded.

The Antillean cebid *Xenothrix*, known from a single specimen from Jamaica (Williams and Koopman, 1952), is markedly differentiated from any known mainland form and must have been derived either from Central or from South America. Beyond those facts it seems unprofitable to speculate about its origin at present.

Besides six endemic[1] Antillean genera (two of doubtful reference) the family Capromyidae is reported to include another genus in coastal Venezuela (*Procapromys;* see Chapman, 1901). The validity of the supposed genus is, however, doubtful, and it may be based on an introduced individual *Capromys* from Cuba (Koopman, personal communication). In any case, the family originated in South America and was already common there in the early Miocene. Again Miocene or earliest Pliocene dispersal from South America is most likely, but again dispersal by way of Central America cannot be absolutely excluded from consideration. The same can be said for most of the Antillean rodents referred to the Echimyidae. Their ancestors certainly came from South America, possibly but very dubiously through Central America.

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[1] *Geocapromys* also occurs on Little Swan Island in the Gulf of Honduras but that island may well be considered Antillean rather than continental. *Geocapromys* may have reached there by human (Carib?) agency but is probably a true native. Dispersal of *Geocapromys* to the Bahamas was also probably natural, but hardly modifies the Antillean endemicity of the genus.

The Puerto Rican *Proechimys* is a special case (see Williams and Koopman, 1951). The genus now occurs, evidently as a Pleistocene immigrant from South America, in Central America up to Nicaragua. The Puerto Rican species seems, however, to have its closest recent relatives in southeastern Brazil, in the subgenus *Trinomys*. Direct derivation from southeastern Brazil is practically impossible, and a wider Pliocene-Pleistocene distribution of *Proechimys (Trinomys)* must be postulated. The Puerto Rican *Proechimys* may be a survivor of the ancestral stem of the Antillean echimyids,[1] or it may be a later (Pleistocene) immigrant. In the former case direct derivation from South rather than Central America is highly probable; in the latter it is less so but still is a decided possibility.

The only known possible West Indian octodontid is *Alterodon* in Jamaica. All other known octodontids occur fossil (from late Oligocene) or living in southern South America. If *Alterodon* is an octodontid, which is far from certain, it must again be assumed that the group formerly occurred farther north on the mainland. There is nothing to prevent extending the purely hypothetical range to Central America, but such extension is less probable than to, say, Colombia.

Finally there is the one known Antillean cricetid, *Oryzomys antillarum* in Jamaica. The genus occurs from New Jersey to southern Patagonia, but the Jamaican form apparently belongs to the *palustris* species group, which now ranges only from New Jersey to Panama and is not likely ever to have been widespread, at least, in South America. Apart from the probably North American ancestral insectivores this is the only Antillean land mammal for which Central American origin is clearly more probable than South American. It is also probably the most recent arrival in the Greater Antilles, even though the species is considered endemic. (The Puerto Rican *Proechimys* discussed above is the only other non-endemic Antillean genus.)

All these facts and inferences must be viewed against the background of the probability that the Central American faunas, and particularly those of the Honduras and Yucatan projections, were almost completely North American until the late Pliocene. The pre-Pleistocene faunas of Central America are virtually unknown except for one of early Pliocene date in Honduras (Olson and McGrew, 1941). That fauna, as now known, is entirely North American in affinities and origin. It contains no possible ancestors, indeed no relatives, of any of the Antillean groups inferred to have reached the islands in Miocene or Pliocene times. From

[1] Miller (1930) postulated their derivation from *Proechimys* long before the discovery of the Puerto Rican form.

the evidence of faunas farther north (Mexico, Texas, etc.) and south (especially Argentina, to a more limited extent Colombia and elsewhere), it appears that only procyonids (from the north in late Miocene) and megalonychids (from the south in the middle Pliocene) crossed the Central American barrier from one continent to another before the late Pliocene (see, e.g., Simpson, 1950). There was a slight beginning of further interchange in latest Pliocene,[1] and then a series of waves of intense interchange in frankly Pleistocene times.

This evidence, although scanty, partly indirect, and therefore inconclusive, makes Central America an unlikely source for the purely South American groups that reached the Greater Antilles after the insectivores and before the one late distinctly Central American rodent, *Oryzomys antillarum*. At least six colonizations are involved. It almost stretches credulity too far to suppose that they came from Central America and yet were all South American stocks that may not even have occurred in Central America at the appropriate times, and none of North American stocks that certainly did occur there.

To sum up:

1. The oldest Antillean land mammals are probably the insectivores, representing two immigrations probably in the early Tertiary from North America.

2. The great bulk of the fauna probably straggled in during the Miocene and Pliocene. A minimum of six different immigrations in this category is indicated by forms now known. All their ancestral stocks certainly came from South America. All the positive evidence now available indicates direct derivation from South America. The evidence bearing on possible migration via Central America is, however, mainly negative, and that possibility is not in any case absolutely excluded.

3. The one known Antillean cricetid is evidently a late Pleistocene or early Recent migrant from Central America to Jamaica. The genus was ultimately derived from the Nearctic region.

LAND OR OVER-WATER DISPERSAL

Earlier zoogeographers mostly assumed that the presence of a rather rich terrestrial biota on the Greater Antilles required the former existence of one or more land bridges from continental areas to the islands. We owe to the genius of Matthew (1915, 1916, 1918, 1919, 1939) the first really serious and reasoned suggestion that the Antillean fauna not

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[1] Probably less extensive than previously supposed. Kraglievich (1952, and unpublished data) suggests that some later mammals have been incorrectly included in the crucial Chapadmalalan faunal lists.

only is consistent with introduction by over-water routes but also is *better* explained by that theory. The over-water theory was heavily attacked by Barbour (especially 1916, see also his anticipatory rejection of the idea in 1914), by Scharff (1922), and by others. It was strongly sustained by still others, notably by Myers (1938) and by Darlington (1938), who reviewed the whole subject with great care and demonstrated that all the objections to over-water introduction of the Greater Antillean fauna are clearly invalid. Since 1938 a majority of students who have made any considerable personal study of the subject have agreed with the essentials of Matthew's views.

When I first drafted the present paper it seemed useless to reopen a question that had been so thoroughly discussed and had, I felt, been settled. Yet it appears that many students still consider this the principal general reason for interest in the Antillean fauna. One of the most recent textbooks of zoogeography (de Beaufort, 1951) not only considers the question still open but also strongly inclines towards the land-bridge theory.[1] It may therefore be useful, if not necessary, to summarize the arguments again.

The main arguments against over-water dispersal and in favor of land-bridge connections are as follows. I have added in brackets a brief statement of the counter-arguments.

1. Over-water dispersal of so many, or of these particular, terrestrial organisms is extremely improbable. [It can be demonstrated that the nature of the fauna is *best* explained by the postulate that colonization was, indeed, highly improbable.]

2. Such dispersal for some Antillean animals is not merely improbable but definitely impossible. Barbour (1916) cites, for example, burrowing amphibians, onychophores, and cyprinodont fishes. ["Impossible" expresses only an opinion that can easily be shown to be fallible in these and other supposed examples. Darlington (1938) and Myers (1938 and 1953) have conclusively demonstrated that over-water dispersal is a real possibility for all the groups of organisms that do, in fact, occur in the Greater Antilles.]

3. "The islands of the Antillean chain have too evenly distributed and homogeneous a fauna for it all to have been fortuitously derived" (Barbour, 1916. [Actually the faunas of the various islands are remarkably heterogeneous. They are striking precisely for their comparative lack of homogeneity. That the distribution is orderly is quite a different point and is, as Darlington (1938) stressed, at least as consistent with over-

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[1] De Beaufort's statement that "Matthew alone denied every continental connection of the Antilles" is curiously incorrect.

water dispersal. "Fortuitously" is a misleading word, because low-probability dispersal still is not truly fortuitous in the usual sense of that word.]

4. There are too many different elements in the fauna for all to have come by " 'flotsam or jetsam' dispersal" (Barbour, 1916). The amphisbaenans, for instance, are said to require eight "practically inconceivable voyages" (*ibid.*). [Quite the contrary: an outstanding peculiarity of the Greater Antillean fauna is that it includes comparatively few groups, many fewer than continental islands or areas on the continents of comparable size and ecological diversity. The necessary number of introductions has also been grossly exaggerated; the amphisbaenans, for instance, require at most three introductions, not eight.]

5. If mammals are rafted at all, they should be far more common on the islands than they are. [That simply reverses the logic of the situation, besides flatly contradicting the previous argument, although Barbour adduced both. The actual abundance of mammals reflects a certain low degree of probable dispersal. They should, indeed, be more common (diverse) if they came on a land bridge.]

6. The supposedly few animals that might really be transported by rafts include some that are conspicuously absent in the West Indies, for example, the "almost semiaquatic" *Basiliscus* (Barbour, 1916). [*Basiliscus* is a poor choice, because rafting is really highly improbable for it (Hecht, personal communication). On the same basis it is, indeed, strange that didelphids or procyonids did not reach the Greater Antilles. But if a land bridge existed, these same failures are far harder to understand than on the theory that colonization was highly improbable in any case and happened to fail in these instances. *Procyon* did reach the Bahamas and the Lesser Antilles, almost certainly by relatively recent rafting from, respectively, North and South America.]

7. The very large percentage of endemic species on each island would not have arisen if "a constant exchange of individuals [by over-water dispersal] from one island to another were taking place" (Barbour, 1914). [Again the facts really better fit the theory of over-water dispersal, which does not involve "a constant exchange" but comparatively rare incidents. A single introduction of one or a few animals could give rise to an isolated colony soon as large as the ecology permitted. Subsequent occasional arrival of related strays would have virtually no influence on the evolutionary divergence of the established population.]

8. "Rafting from island to island could certainly not have occurred" (Barbour, 1916), yet the smaller islands have merely an attenuated representation of groups that also occur on the larger islands. Why should just those groups and no others have succeeded in over-water

transport from the mainland repeatedly to larger and smaller islands? [It is agreed that in most cases, if not all, the few mammals of the small islands were derived from the nearest of the four main islands. This would be likely whatever the means of dispersal and has little or nothing to do with how the animals reached the main islands. Over-water dispersal from island to island is, furthermore, by no means ruled out.]

9. The islands may well have had a balanced fauna of continental type that has simply been impoverished by the vicissitudes of island life. The ungulates, for instance, may have been exterminated by repeated flooding of the lowlands (Scharff, 1922). [The fauna as a whole is rather rich. It is poor only in comparison with areas that did have land connections. It does not seem to be impoverished but seems simply to have evolved from comparatively few ancestral species. It is, as Darlington says, an accumulation, not a residue. The mammals, to be sure, are now impoverished but that occurred quite recently, in large part since man reached the islands. It seems, moreover, virtually impossible to imagine what vicissitudes of island life could have eliminated all the carnivores, for instance, while suitable prey for them continued to be abundant.]

So much for the principal arguments against over-water dispersal and the reasons why those arguments do not weigh heavily at least. Here are some of the most impelling positive arguments in favor of over-sea dispersal:

1. The fauna represents a remarkably small number of major groups or ancestral stocks in comparison with faunas on adjacent mainlands. The absence of so many of the most abundant and ecologically suitable mainland groups is inexplicable if there was a land bridge.

2. The comparative poverty of the fauna cannot be explained by insular conditions. Trinidad, for instance, has a much richer fauna, although it is smaller and no more varied than any one of the main islands of the Greater Antilles (Darlington, 1938). The most reasonable explanation is that Trinidad was and the Greater Antilles were not accessible by a land route.

3. The stocks that are present all belong to groups for which over-water transport (by a variety of different means) is a distinct possibility.[1]

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[1] The dangers of second-hand study (from which I cannot hope that this paper is wholly free) are amusingly illustrated by a remark in de Beaufort (1951, p. 140). He says of the "megalonyxids" (*sic!*) that "it is hard to imagine these huge animals arriving in the West Indies on rafts!" Obviously he thought of the Antillean megalonychids as giant ground sloths on the style of *Megatherium*. Actually they are quite small, the largest of the several kinds being about the size of sheep. Their ancestors who made the trip may have been about the size of the living tree sloths and were, moreover, probably at least semi-arboreal. That such animals were often swept out to sea on floating trees is more likely than not.

Birds, bats, and insects are especially varied and are demonstrably apt at over-seas colonization. Similar stocks of these groups occur on innumerable islands certainly never reached by land bridges. The probabilities vary greatly from group to group, but average probability of over-water transport is clearly much greater for the island stocks than for the whole faunas of adjacent continents. That dispersal was indeed over water is the only reasonable explanation for this difference.

4. Groups for which any form of over-water transport is really extremely unlikely, such as the ungulates among mammals, are indeed absent. There are no really large animals. (On the largest that did reach the islands, see footnote on p. 9.) Contrary to statements widespread in the early literature, there are no strictly fresh-water fish (Myers, 1933; see also Darlington, 1948).

5. The fauna is ecologically unbalanced. The most striking example is the fact that the mammals include no carnivores. There are other niches abundantly filled on the adjacent continents and potentially present on the islands but empty in the latter. It is virtually inconceivable that a land bridge could have filtered out all carnivores and all members of other niches empty on the islands. Over-sea transport, with its low overall probability and its random selection of groups of equal probability, is the only reasonable explanation.

6. It is improbable that the fauna came from one geographic source. The point is debatable and some authorities think most, if not all, came from Central America, but there is good evidence also for derivation of some elements from farther northeast in North America and of some direct from South America. If that is correct, the land-bridge theory must visualize at least three bridges, each of which was crossed by just a few stocks. That multiplies the previously mentioned difficulties to such a point as to border on absurdity.

7. There is evidence that the ancestral stocks reached the islands one or a very few at a time, scattered through a geologically long span. The land mammals, for instance, seem to have evolved from a few (probably nine, possibly one or two more) separate original colonizations during 30 million years or probably even longer. That is characteristic of waif or sweepstakes dispersal. It is incomprehensible in terms of land bridges.

8. There is an extraordinary degree of endemism in each of the various islands, still more in the islands as a whole in comparison with the mainland. Long separation of the large islands from one another and of all from the mainland is indicated. Nevertheless the degrees of endemism vary greatly in different groups. There are endemic families, but there are also non-endemic genera. It is necessary to conclude that some groups were isolated on particular islands while other groups were

not isolated on those same islands (or reached those islands while the other groups were isolated there). Again this is just what would be expected of waif dispersal and is virtually inconceivable with any system of land bridges.

It may be added that ocean currents and hurricane tracks are and probably have long been favorable to the rare introduction of waifs to the islands. (On storm tracks, see Darlington, 1938.) It may again be emphasized that rare colonization over a long period of time best fits the facts.

The direct geological evidence is mostly neutral: it neither suggests nor strongly negates the possible presence of land bridges. Geologists who have indicated such bridges on paleogeographic maps (e.g., Schuchert, 1935) have done so entirely on what they believed to be the zoological evidence. The strictly geological evidence does not suggest the presence of land bridges (Woodring, 1954).

On the basis of present evidence, the over-water dispersal theory is so much the more probable that the land-bridge theory is not worthy of further serious consideration except in the unlikely event of the discovery of wholly new evidence favoring it. This does not exclude the possibility of some past bridges between islands within the group. However, the land mammals, at least, seem on the whole to give evidence against even that possibility.

MIGRATION ROUTES

On the map, the Lesser Antilles appear to be an almost ideal set of stepping stones for introduction of South American animals into the Greater Antilles. Nevertheless that route can be almost certainly ruled out. The few living and even fewer known prehistoric land mammals of the Lesser Antilles show almost no special resemblance to those of the Greater Antilles. There are no forms in the Lesser Antilles that could possibly be ancestral to any of those in the Greater Antilles. Such as it is, the fauna of most of the Lesser Antilles is simply a highly attenuated extension of the recent fauna of Trinidad and eastern Venezuela. The species are mostly endemic, as would be expected, but there are no endemic genera except at the very end of the chain.

The extinct endemic *Amblyrhiza* on Anguilla and St. Martin is exceptional in the Lesser Antilles. It is related to the heptaxodontids of Puerto Rico, whence its ancestors doubtless came. It is not suggestive of any migration in the opposite direction. *Megalomys,* a recently extinct endemic[1] on near-by Barbuda, Martinique, St. Lucia, and perhaps

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[1] Endemic if the genus is accepted. It is close to, and often considered synonymous with, the widespread *Oryzomys.*

Tobago, is a probable derivative from South America that did not, as far as known, reach Anguilla or Puerto Rico. These forms suggest that Anguilla and St. Martin, geographically in the Lesser Antilles, could be placed zoogeographically in the Greater Antilles, but zoogeography based on a single form has little or no meaning. In any event, these facts do not modify the conclusions that the Lesser Antilles have not been a migration route to the Greater Antilles for land mammals.

It has been noted that the Antillean insectivores were probably of North American origin. If that is correct, they came either from southeastern United States or from Central America. In the early Tertiary the gap north of Cuba was much wider than it is now, and the current probably set away from the islands. There was probably a peninsula from present Honduras extending onto the present Nicaraguan Swell (see Woodring, 1954, fig. 2). On an almost wholly conjectural basis, that may be postulated as a possible point of origin for the ancestral Antillean insectivores.

If, as has been shown to be likely, the Miocene-Pliocene migrants came directly from South America, they were probably rafted from what is now Colombia. The great Magdalena river system has existed since the Miocene at least. Offshore currents there now eddy into the Caribbean current and hence past Jamaica and Cuba. Before the closure of the Panamanian and Colombian gaps there was probably more westward flow, to the Pacific, but recurrent flows back towards western Greater Antilles probably also existed. (Again, see map in Woodring, 1954, and his citations.)

Introductions of waifs to Jamaica and Cuba by this route would be highly improbable, but they would be possible, and that is all that the theory demands. Separate invasions of those two islands are indicated by the evidence. Introduction into Hispaniola would be no more and probably even less likely. Direct dispersal to Puerto Rico would be so extremely improbable as to be almost, but not quite, ruled out. In fact all the known fauna of Hispaniola could have reached there in part via Jamaica and in part via Cuba. Much if not all of the known fauna of Puerto Rico seems to have come from Hispaniola. On the other hand it is improbable that either Jamaica or Cuba derived a great part of its fauna from any other island. The evidence is exiguous, as is so much of the evidence bearing on this subject, but it does agree with the hypothesis.

It might be asked why, if there was waif dispersal from Colombia to the western Antilles during the late Tertiary, there was not also some rafting of South American groups to Central America. The answer is that there was. Megalonychids, one of the groups rafted to Cuba, were

also rafted to Central America and hence had already spread northward in the Pliocene. Some South American rodents and primates may also have been in Central America before closure of the gaps; the negative evidence here is far from impelling. Negative evidence of their absence in the Miocene or Pliocene of the United States does have some weight. Although the land route is now open to them, none of the South American relatives of West Indian mammals have ranged into the United States. Ecological rather than geographic barriers doubtless prevented their expansion northward from Central America in the Miocene and Pliocene, if they were there then, as they did in the Pleistocene and Recent. The Antilles, on the other hand, had no ecological barriers against establishment of these mammals.

It remains possible that some ancestors of Antillean mammals were rafted first from Colombia to Central America and then to Jamaica or Cuba. The negative evidence is not impressive, but the hypothesis is unnecessary, at least, to explain what is now known. A further consideration that has no great weight but that does add a bit of support for the hypothesis of direct derivation from South America is that Central American river systems may have been less likely to produce rafts than the Magdalena system.

The hypothesis that most of the Antillean land mammals came directly from South America does not conflict with strong evidence that many other Antillean animals, especially those that could be air borne, came from Central America. The means of dispersal were different.

The Jamaican *Oryzomys* evidently came from Central America, and its remoter ancestors were certainly North American. The immediate place of origin was probably Honduras-Nicaragua. It is just possible that the introduction, although prehistoric, was by human agency. Otherwise rafting is the most likely explanation, although air-borne introduction by a hurricane is possible. That does not necessarily conflict with the previous suggestion that rafting from Central America is improbable. A high degree of improbability must be postulated to explain why no North American mammal except *Oryzomys* (and perhaps the much earlier insectivores) are known ever to have reached the Antilles from Central America. The fact that no other and no earlier typically or exclusively Central American stock ever reached the Greater Antilles (as far as known) still does add materially to the likelihood of direct derivation of most stocks from South America.

DISPERSAL WITHIN THE GREATER ANTILLES

All but one of the Antillean species are endemic to a single major island (in some cases with spread to adjacent small islands). Most of the

genera are similarly endemic. Exceptions (see table 1) are: *Nesophontes* on Cuba, Hispaniola, and Puerto Rico; *Solenodon* on Cuba and Hispaniola (but the species are so distinct that Cabrera, 1925, does separate them generically); *Acratocnus* on Cuba, Hispaniola, and Puerto Rico; *Megalocnus* on Cuba and Hispaniola; *Geocapromys* on Jamaica and Cuba (also the Bahamas and Little Swan Island in the Gulf of Honduras); and *Isolobodon* on Hispaniola and Puerto Rico.

The high degree of endemicity within the islands (table 2) and the low degree of faunal resemblance between any two of them (table 3)[1] vir-

TABLE 2

DEGREES OF ENDEMISM (IN PER CENT) IN THE GREATER ANTILLES

	Families[a]	Genera
Compared within the islands		
Jamaica	60[b]	86
Cuba	0	44
Hispaniola	0	50
Puerto Rico	0	62
Whole group compared with mainland	33	92

[a] The Heptaxodontidae are considered endemic in the Antilles, although the family occurred at an earlier date in South America. The family Megalonychidae is not considered endemic.

[b] The three families endemic to Jamaica within the islands do all occur on the mainland.

tually demand long separation of the present island masses. (The probability that some of them were earlier further subdivided into two or more separate islands has no bearing on this point.) Negative evidence also has some weight here. The apparent absence of echimyids and megalonychids from Jamaica, of heptaxodontids from Cuba, and of capromyids other than the doubtful *Isolobodon* from Puerto Rico may be canceled by new discoveries at any time, but as of now it appears as though no land dispersal of mammals had occurred between any two of the islands.

Although Darlington (especially 1938) has strongly opposed land-bridge connection between the islands and the mainland, he does think it likely that there were land bridges within the group from Hispaniola separately to Cuba and to Jamaica. He reasonably concludes that over-water dispersal should tend to produce faunal similarities inversely pro-

[1] In this index of faunal resemblance C = number of taxa in common and N_1 = number in the smaller of the two faunas. On the rationale of this index, see Simpson (1947).

portional to the widths of the water barriers. Jamaica is nearer to Cuba than to Hispaniola, but Darlington considers its fauna as more like that of Hispaniola. He therefore postulates that the Jamaica-Cuba resemblance is better explained by a land route by way of Hispaniola. The land mammals do not support this view. For these three islands the sequence of decreasing resemblance of land mammals (table 3) is His-

TABLE 3

FAUNAL RESEMBLANCES WITHIN THE GREATER ANTILLES

	Jamaica	Cuba	Hispaniola	Puerto Rico
$100C/N_1$ for families				
Jamaica	100	20	0	0
Cuba	20	100	80	50
Hispaniola	0	80	100	100
Puerto Rico	0	50	100	100
$100C/N_1$ for genera				
Jamaica	100	14	0	0
Cuba	14	100	44	25
Hispaniola	0	44	100	38
Puerto Rico	0	25	38	100

paniola-Cuba, Cuba-Jamaica, Jamaica-Hispaniola. That is precisely the sequence of increasing width of the existing water barriers and therefore, on Darlington's own premises, agrees with the hypothesis of over-water dispersal. As noted above, the known distribution of the families also and more strongly opposes a Cuba-Hispaniola-Jamaica connection. If, as Darlington states without details, the Jamaican fauna as a whole (other than the land mammals) is more like that of Hispaniola than of Cuba, this really would not rule out over-water dispersal. The difference in widths of the water barriers is not very great (about 100 vs. 125 miles) and could readily be counteracted by the history of currents, winds, and storms, and even by mere chance.

There clearly has been dispersal among the islands, and the present evidence suggests that this was waif dispersal. The non-endemic genera thin out both ways (south and east) from Cuba. Hoffstetter (1955) suggests that all four megalonychids originated in Cuba, two hence reaching Hispaniola, and one of those going on to Puerto Rico. The insectivores could have had a similar history, both stocks spreading from Cuba to Hispaniola and only *Nesophontes* going on to Puerto Rico. Dispersal with no more than specific differentiation is not likely to be much if any older than the Pleistocene.

Heptaxodontids were dispersed across Jamaica-Hispaniola-Puerto Rico, but so long ago that all the genera are now endemic. The same, as within the islands, is true of the echymyid dispersal across Cuba-Hispaniola-Puerto Rico. Those dispersals could be early Pleistocene, but some time in the Pliocene seems more likely. A dispersal of about equal antiquity is indicated for capromyids across Jamaica-Cuba-Hispaniola (and Puerto Rico if *Isolobodon* is a capromyid), with another later dispersal of *Geocapromys* between Cuba and Jamaica. The direction of those dispersals is uncertain. The minimal hypothesis would be that all occurred from Jamaica (at least heptaxodontids and perhaps capromyids) and Cuba (at least megalonychids and echimyids and perhaps capromyids).

Most of the Puerto Rican mammals probably came from Hispaniola, and all of them may have. A possible anomaly is the presence on Puerto Rico only of the most primitive echimyid, *Proechimys,* but the negative evidence of its absence from Hispaniola is not impelling. Hispaniola could have derived all its mammals from Jamaica and Cuba but not, on present evidence, from just one of those two islands. This possibility is, however, somewhat less impressive than the possible derivation of all Puerto Rican mammals from Hispaniola. It does seem possible that the Cuban echimyid (*Boromys*) is of Hispaniolan ancestry. It is extremely unlikely, however, that either Cuba or Jamaica derived all its mammals from any others of the Antilles.

It is thus concluded, as a tentative theory, that:

1. Jamaica and Cuba each received some stocks from mainland sources. They may have received some also from Hispaniola, but that is not a necessary conclusion from the evidence.

2. Hispaniola probably derived its mammals from Jamaica and Cuba (both), but direct derivation from the mainland is not excluded for one or two groups.

3. Puerto Rico probably derived its mammals from Hispaniola, but direct mainland derivation for one group (echimyids) is possible.

The basic theory or minimal hypothesis, then, would have four or five colonizations from the mainland on Jamaica, of which three (cebids, cricetids, ?octodontids) are not known to have spread farther, one (heptaxodontids) spread to Hispaniola and then Puerto Rico, and the other possible one (capromyids) spread to Cuba and to Hispaniola unless it first landed on Cuba. *Isolobodon,* a possible capromyid, further spread from Hispaniola to Puerto Rico. Cuba, on this hypothesis, would also have either four or five original colonizations, three (nesophontids, megalonychids, echimyids) spreading to Hispaniola and hence to Puerto Rico, one (solenodontids) to Hispaniola only, and the other possible one (capromyids) to Jamaica and to Hispaniola unless its first colonization

was on Jamaica. The most probable modification of this hypothesis would be to postulate that one or two stocks (echimyids and possibly capromyids) first colonized Hispaniola or Puerto Rico and then spread between those two islands and to Cuba.

Regardless of the direction in which dispersal has occurred, it is fairly evident that intermigration has been greatest between Cuba and Hispaniola, less between Hispaniola and Puerto Rico, and least between Jamaica and either Cuba or Hispaniola. There are various uncertainties in the exact figures, but on present evidence it would be reasonable to postulate as minima about six dispersals for Cuba-Hispaniola, four for Hispaniola-Puerto Rico, one for Cuba-Jamaica, and one for Jamaica-Hispaniola.

These possible or probable lines of dispersal are of sufficient interest to warrant brief further analysis in terms of general principles bearing on linear dispersal patterns.

LINEAR DISPERSAL

Dispersal of animals along a chain of islands or along an isthmus or peninsula tends to occur in linear sequence. Either isthmus or peninsula can break up into a line of islands after dispersal has occurred, and, with various possible complications, that would be the history in the Greater Antilles if land connections were involved.

In linear dispersal, the numbers of groups colonizing the area and the diversity of animals in a given regional unit, such as an island, are influenced but various factors, among which the following seem to be most important:

1. The linearity itself and the direction of dispersal. Even when dispersal is wholly or dominantly in one direction, the number of colonizations may be the same throughout if no significant barriers are present. If there are significant barriers, the number of colonizations will tend to be progressively smaller in the direction of dispersal, and this effect will be stronger the greater the barriers involved. When there is a progressive decrease in numbers of colonizations, there will also tend to be a corresponding decrease in basic diversity, most likely at high taxonomic levels, to some extent genera, but especially families and higher groups. For smaller taxa, especially species and to some extent genera, this tendency will be secondary to and perhaps wholly counteracted by, other factors, especially 3 below.

2. Lag. The time taken for dispersal is probably never significant in comparison with the time involved in sequential speciation, unless quite strong barriers occur. If there are such barriers, the introduction of a group at the far end of the sequence may be significantly later than at the

near end. It is evident that if other things are equal groups will be more diverse the longer they have been in a given area and more progressively changed the longer they have been adapting to a sequence of different environments. Further, the older the group, in the sequence, the more likely that it will occur towards the terminal regions.

3. Size and ecological diversity of regional units. It is well established that a fauna tends to be more diverse, to include larger numbers of taxa, the larger and more ecologically varied the region covered. Area and ecological diversity are not necessarily closely correlated, but they tend to be so, especially in such cases as the islands of the Greater Antilles, not markedly different in topography and all in the same climatic zone. In a sequence without marked barriers, these effects tend to dominate. A small area (such as an island remnant of a formerly continuous land route) near the beginning of a linear sequence may have fewer lower taxa, at least, than a large area near the end. When significant barriers occur, their tendency to reduce diversity towards the terminal area will interact with and may counteract the effects of size and ecological diversity. The latter factors have little effect on numbers of colonizations except to the (sometimes considerable) degree that small area and ecological uniformity in themselves constitute filters or barriers.

4. Barriers. Part of the interplay of barriers with other factors has been noted in connection with the preceding factors. A sequence of strong and approximately equal barriers, such as straits of more or less comparable width in a string of islands, progressively reduces the numbers of colonizations along the chain and hence also the basic or higher taxonomic level diversity, at least. The greater the barrier, the stronger the effect. Differences in strength of barriers may overshadow the effect of sequential reduction. For instance, if the first step in sequence is across a great barrier (such as from the mainland over water to Cuba) and a second step is across a much smaller barrier (such as from Cuba to Hispaniola), more dispersal may occur across the second step than across the first. Nevertheless the groups taking the second step must obviously be derived from those that had previously taken the first. They may be more numerous, but they must be derived from the same or a smaller number of original stocks.

Application of these principles to the Greater Antilles is complicated by the fact that they are not, in fact, in simple linear sequence. Jamaica-Cuba-Hispaniola form a triangle, with Puerto Rico adjacent to one of the angles (Hispaniola). They may, however, be analyzed as a sequence with a double first term (Cuba-Jamaica) or as two interacting linear sequences: Cuba-Hispaniola-Puerto Rico and Jamaica-Hispaniola-Puerto Rico. In the latter case, Cuba-Jamaica or Jamaica-Cuba may be

considered as a third, short sequence. In the history as a whole, each of these sequences also has the mainland as a first term.

The hypothesis that colonization was sequential and in the order named is supported by the fact that all Puerto Rican families also occur on Hispaniola and all Hispaniolan families either on Cuba or on Jamaica. Details are evident in table 1 and discussed in the previous section.

Table 4a does not show any clear tendency towards linear decrease in

TABLE 4

DIVERSITY AND COLONIZATIONS IN THE GREATER ANTILLEAN
FAUNAS OF LAND MAMMALS

a. Known Numbers of Taxa

	Jamaica	Cuba	Hispaniola	Puerto Rico
Families	5	5	6	4
Genera	7	9	10	8

b. Approximate Numbers of Taxa per 1000 Square Miles

	Jamaica	Cuba	Hispaniola	Puerto Rico
Families	1.1	0.1	0.2	1.2
Genera	1.6	0.2	0.3	2.4

c. Probable Numbers of Stocks Originally Colonizing the Islands

	Jamaica	Cuba	Hispaniola	Puerto Rico
From all sources . . .	5	5	7	4
From the mainland . .	4(3–5)[a]	5(0–5)	0(0–6)[b]	0(0–4)
From other islands . .	1(0–2)	0(0–6)[b]	7(0–7)	4(0–4)

d. Numbers of Taxa and of Colonizations for Families Known in Cuba

	Cuba	His-paniola	Puerto Rico	Cuba	Jamaica
Families	5	5	3	5	1
Genera	9	9	6	9	1
Colonizations[c] . . .	5	6	3	5	1

e. Numbers of Taxa and of Colonizations for Families Known in Jamaica

	Jamaica	His-paniola	Puerto Rico	Jamaica	Cuba
Families	5	2	1	5	1
Genera	7	3	2	7	2
Colonizations[c] . . .	5	2	1	5	1

[a] Numbers outside parentheses are those considered most likely. Numbers in parentheses are those considered minimal and maximal on available evidence.

[b] The apparent discrepancy between the probable maxima for a given source and the probable total for all sources is due to doubt as to original place of differentiation of Antillean Megalonychidae. They apparently represent one colonization on the island first reached from the mainland but two (by different genera) on another island, either Cuba or Hispaniola.

[c] Total number considered most likely from any source.

diversity. There is a small radial decrease from Hispaniola to each of the other islands. The hypothesis that Hispaniola was the center of dispersal to all of the other islands cannot, however, be sustained. On other grounds, already made clear, derivation of the whole fauna from Hispaniola is probable for Puerto Rico but highly improbable for Cuba and apparently impossible for Jamaica. The hypothesis that effects of dispersal on faunal diversity are here swamped by effects of size and ecological diversity must also be discarded. The two much largest islands, Cuba and Hispaniola, do indeed have slightly more diverse faunas than the two smallest, Jamaica and Puerto Rico, but the degree of association is far from significant. In fact the diversity is so nearly the same on all the islands that the number of taxa per unit area (table 4b) is simply inversely proportional to the sizes of the islands. This, incidentally, is strong further evidence against the view that the separate island faunas are residual or relict from what was once a fauna general to the group as a whole. In the latter case, an approximately constant number of taxa per unit area would be expected.

If, now, the numbers of taxa are analyzed in terms of two different (but partly additive) sequences, reduction in diversity is fully confirmed for Jamaica-Hispaniola-Puerto Rico (table 4e) and partly for Cuba-Hispaniola-Puerto Rico (table 4d). Hispaniola does have all the families known from Cuba and the same number of genera in those families. This is, however, consistent with the hypothesis of dispersal mostly or entirely from Cuba to Hispaniola, if the following reasonable and probable assumptions are made: dispersal from Cuba to Hispaniola was relatively frequent, and local differentiation up to the level of genera was favored on Hispaniola, one of the largest and most varied islands.[1] The slightly greater diversity of the Hispaniolan than of the Cuban fauna seems adequately explained by those considerations plus the fact that Hispaniola also received colonists from Jamaica which did not reach Cuba. It is neither necessary nor indicated, on available data, to conclude that Hispaniola was a source of many or indeed of any mammalian stocks for any other island except Puerto Rico.

There is a large subjective element in estimates of numbers of original colonizations (table 4c, d, and e), but these estimates are also consistent with the hypothesis of two extended and partly coinciding linear sequences: mainland-Cuba-Hispaniola-Puerto Rico and mainland-Jamaica-Hispaniola-Puerto Rico, with significant barriers at each step. Puerto Rico clearly had fewer colonizations than any other island. Hispaniola

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[1] Approximate areas in thousands of square miles are: Cuba, 44.2; Hispaniola, 29.8; Jamaica, 4.5; Puerto Rico, 3.4.

had fewer colonizations involving families present on Jamaica than did Jamaica itself. That Hispaniola had more colonizations, in all, than Jamaica is explicable on the basis that most of those on Hispaniola came from Cuba. That it also had more than Cuba, even in families also present on Cuba, is explained in part by colonization also from Jamaica and in part by separate colonizations from Cuba of groups differentiated within Cuba following single colonizations of their ancestors from the mainland. There is the further element that mainland-Cuba dispersal was across a much wider barrier and may therefore have been even less frequent than Cuba-Hispaniola dispersal.

As to effects of what is called "lag" above, these are not clear over all, but there is some suggestion of them, and the evidence is at least not inconsistent with the sequence of dispersal and barriers here proposed. All groups old in the Antilles have spread to three of the islands, and the Capromyidae have spread to all four, if *Isolobodon* belongs in that family. On Puerto Rico, postulated as the end of both branches of the double linear sequence, all genera belong to families also present on two islands earlier in the sequence, either Hispaniola and Cuba or Hispaniola and Jamaica. Of the three Puerto Rican genera non-endemic as within the islands, two (*Nesophontes* and *Acratocnus*) occur on both Hispaniola and Cuba and one (*Isolobodon*) on Hispaniola. The thinning out of megalonychids in the sequence Cuba-Hispaniola-Puerto Rico has already been mentioned. What seems to be the most recent arrival in the Antilles (*Oryzomys*) is confined to the postulated beginning of one of the sequences. As noted above, the Puerto Rican *Proechimys* may tell against the postulated lag effect, but it does not necessarily do so and is in any case insufficient to establish more than a possible exception to the overall sequence.

Aside from the two main, overlapping sequences of dispersal, the only clear evidence for another sequence is mainland-Cuba-Jamaica for the Capromyidae. (Mainland-Jamaica-Cuba is also possible but less probable.)

It is quite possible and indeed probable that the theory developed here will eventually prove to be too simple. Movement along these sequences may well have been two-way at different times and considerably more complex. Nevertheless it seems that the simpler theory can account for all the facts now known, and that it is likely to explain most, even if eventually not all, of the dispersals.

ZOOGEOGRAPHIC STATUS OF THE GREATER ANTILLES AS A WHOLE

Virtually all zoogeographers have followed Sclater in including the

West Indies with Central (= Tropical North) America and South America in Neogaea, or the Neotropical region. Only recently has any important dissent appeared. Schmidt (1954) would associate the Greater Antilles with North America in the Holarctic. His reasons are (1) that the Greater Antillean fauna is closest to that of Central America, and (2) that Central America belongs historically with North and not South America. It is demonstrated herein that 1 is not true of the land mammals. Regarding 2, the statement is probably correct for most of the Tertiary, at least, but it is not pertinent to the present topic for two reasons. First, as regards the West Indies it would be pertinent only if their fauna were also historically connected with North America. That is certainly not true of the bulk of the land mammals. All of those except the two genera of insectivores and *Oryzomys* (only 12% of the known genera) are obviously of South American origin, whether they reached the islands by way of Central America or more directly. Second, the only possible objective way to define zoogeographic regions is by their faunal characteristics at a particular time. That Central America once upon a time had a purely North American fauna does not alter the fact that its fauna now resembles that of South America much more than it does that of temperate North America. It was in a Neartic region, but it is in the Neotropical region. (I hope to go into that point more fully in a separate study of the zoogeographic status of Central America.)

Table 5 shows the regional resemblances of the Greater Antillean land mammalian faunas. The resemblances in terms of genera are hardly significant because of the extreme generic endemicity of the Greater Antillean fauna. The comparison by families shows much less resemblance to the Nearctic region (temperate North America) than to the Neotropical region (South America plus Central America or more exactly tropical North America).[1] As between Nearctic and Neotropical regions, the classic zoogeographers were obviously right in putting the West Indies in the Neotropical, as far as the land mammals are concerned.

Within the Neotropical region, the Greater Antillean fauna is distinctly more like that of South America than that of Central America, contrary to a widespread impression. This is even true of Jamaica, which has the greatest resemblance to Central America. In fact, however, the

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[1] In compiling this table I counted the Megalonychidae as a recent family throughout, because they seem to have survived into the geological epoch Recent in the West Indies and both the Neotropical and Nearctic regions. The Heptaxodontidae are counted as recent only in the West Indies. Rejection of the Megalonychidae from the continental recent faunas or inclusion of the Heptaxodontidae in South America would increase the resemblance to the Neotropical region and specifically to South America.   .

TABLE 5

FAUNAL RESEMBLANCES OF THE GREATER ANTILLES
AND THE MAINLAND

	South America	Tropical North America	Temperate North America
$100C/N_1$ for families			
Jamaica	80	60	20
Cuba	60	40	20
Hispaniola	50	33	17
Puerto Rico	50	50	25
Whole group	67	44	22
$100C/N_1$ for genera			
Jamaica	14	14	14
Cuba	0	0	0
Hispaniola	0	0	0
Puerto Rico	12	12	0
Whole group	8	8	4

resemblance is far from close in any case. The maximal resemblance of the whole Greater Antillean fauna to any mainland faunas is less than the resemblance of some local faunas almost universally placed in different regions, for instance those of Colorado and of Neotropical Mexico. The latter comparison has the index $100C/N_1$ for families 67 and for genera 43. Even between Colorado and the Guianas the generic index is 16, twice as large as between the Greater Antilles and South or Central America. Apart from flat measures of resemblance, the whole makeup of the West Indian fauna is highly peculiar and extraordinarily unlike that of any mainland region.

The fauna of the Greater Antilles is indeed so distinctive that on this basis that island group fully merits designation as a separate major faunal region all by itself. But it is also an extremely heterogeneous region. Table 3 shows the same measures applied to faunal resemblances among the four major islands. All these values are also remarkably low, quite within ranges of some resemblances between established separate major faunal regions. Thus each island merits, if judged on this basis, designation as a separate major faunal region. This tends towards a *reductio ad absurdum.*

In fact the whole concept of faunal regions, although an excellent descriptive device when applied to continental areas that do in fact share large regional faunas, simply is not applicable to many smaller areas such

as those of the Greater Antilles. They do not now have and never have had a balanced regional fauna such as those on which the classical faunal regions are based.

Some islands clearly are populated by more or less attenuated marginal parts of a continental fauna. They can then usefully be referred to the corresponding faunal region. This is true of Trinidad and even of the Lesser Antilles, the few land mammals of which are almost all truly Neotropical. The British Isles, Japan, Sumatra, and New Guinea are examples in other faunal regions. Other islands have not merely attenuated faunas but faunas that are unbalanced or ecologically incomplete, that include few major groups (e.g., orders), that are composed of elements of apparently quite distinct ages, and that have an extraordinary degree of endemism at levels from genera upward. The Greater Antilles and Madagascar are the classic examples for land mammalian faunas. Beyond the reach of mammals, the Hawaiian Islands and the Galápagos are other classic examples for their birds and some other faunal elements.

A few doubtful cases exist, but most islands can be put unequivocally in one or the other of those two categories. This fact has of course been noticed long since, sometimes as a distinction between continental and oceanic islands, although the zoogeographic categories do not quite coincide with usual geological definitions (see Mayr, 1940). The islands with attenuated continental faunas are, for the most part, those that were connected with a continent during the Pleistocene. That is not, however, invariably true. The Lesser Antilles (excluding Trinidad) were almost certainly not connected with South America in the Pleistocene but do have an attenuated continental Neotropical fauna. New Britain and the Solomon Islands seem to be another example of an attenuated continental (here Australian) fauna without a Pleistocene land connection. The crucial factors in the quite different cases such as the case of the West Indies seem to be the long existence of a major water barrier which has nevertheless been crossed by separate faunal elements scattered through a geologically extensive span of time. It is, of course, further necessary that the islands in question must have been continuously above water for the pertinent span of time.

As to the zoogeographic classification of such isolated island units with abnormal faunas, there seem to me to be only two fully logical alternatives. We can recognize that each such island, or in some instances group of islands, is in fact as distinctive as one of the classical continental zoogeographic regions. It has been pointed out that this alternative would almost demand recognition of Jamaican, Cuban, Hispaniolan, and Puerto Rican regions, each coordinate with the Nearctic and Neotropical regions. The other alternative is to confine the designation of regions to the

continents and the islands that really share their faunas and to exclude the other islands from the regional system. This may not seem tidy to those who feel that every spot of land must be included in some defined zoogeographic region, but it is logical, and it not only fits but also helps to explain the facts. Preferring this alternative, I would consider the Greater Antilles a special case, to be considered as such on its own merits. These islands belong neither to the Neotropical nor to the Nearctic region. That their land mammals are mainly derived from the Neotropical region is an interesting and important point, but it has nothing to do with the descriptive designation of the recent zoogeographic situation. The recent Neotropical fauna is mostly derived from the Nearctic, but it would not be useful to conclude that the Neotropical region should therefore be included in the Nearctic.

Finally it may be observed that the Greater Antilles are a zoogeographic dead end. They have not served as a dispersal route between any other regions,[1] nor have they been a source for land mammals in any other faunas. The latter point may at first sight seem possibly contradictory of some of the theses of this essay. If there was over-water dispersal from South and Central America to the Greater Antilles why was there none in the opposite direction or to southeastern United States? Currents and storm tracks favor one-way transport from South or Central America to the Greater Antilles. They by no means preclude transport to southern United States, but here there is the additional factor that until the end of the Pleistocene the over-water distance was much greater than at present.[2] In all three cases there is the crucial fact that North, Central, and South America have been continuously occupied by large, balanced, and ecologically essentially complete or closed faunas. The chances that waifs from the islands would survive in such communities are almost negligible. On the other hand most if not all waifs (at least those of just such stocks as did colonize the islands) would find in the Greater Antilles what was essentially an ecological vacuum for them. Once the hazardous trip was over, survival and expansion would be much more likely than not. That mainland-West Indian colonization

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[1] This and the following generalizations are not significantly modified by the extension of *Geocapromys* to the Bahamas or of the ancestors of *Amblyrhiza* to the extreme northern end of the Lesser Antilles.

[2] In fact it is quite possible that a few animals more apt than land mammals for hurricane transport have managed to invade the United States from the West Indies. This whole discussion of the zoogeographic status of the islands applies primarily to the land mammals. I believe that it also does apply in a more general way to the faunas as a whole, but with various modifications and exceptions because of the different means of transport and requirements for colonization.

was mainly if not wholly one-way is thus readily explicable on the theory of waif transport. Incidentally, this would be far less likely if there was a land bridge, and it is another bit of evidence against that theory.

ADDENDUM

After the present paper was in press, Mr. Samuel B. McDowell, Jr., kindly communicated the following observations, which he will publish in detail. (1) There is evidence of special relationship between *Nesophontes* and *Solenodon*. This might justify union of the families Nesophontidae and Solenodontidae and in any case would suggest that they represent a single colonization from the mainland rather than two. (2) The genus *Alterodon* may not be valid, and evidence for the occurrence of Octodontidae in the West Indies is poor or perhaps erroneous.

These changes would alter some of the precise numbers in the preceding tables and discussion, but would not affect any of the conclusions. Reduction in the number of dispersals from the mainland and removal of the anomalous record of an otherwise far southern group (Octodontidae) would tend rather to strengthen the theses of this paper.

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